Drivers of large-scale geographical variation in sexual systems of woody plants

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Abstract: Sexual systems strongly influence angiosperm evolution and play important roles in community assembly and species responses to climate change. However, geographical variation in proportions of different sexual systems (dioecy, monoecy and hermaphroditism) in response to changes in climate, life-history traits and evolutionary age remains poorly understood. Here, we map the geographical variation in proportions of different sexual systems and hypothesize that the prevalence of hermaphrodites increases with aridity owing to their advantages in colonizing harsh environments, whereas dioecy is most successful in humid regions with tall-canopy vegetation and old floras.

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Running title: Geographical drivers of plant sexual systems

ABSTRACT

Aim: Sexual systems strongly influence angiosperm evolution, and play important roles in community assembly and species responses to climate change. However, geographical variation in the proportions of different sexual systems (dioecy, monoecy, and hermaphroditism) in response to changes in climate, life-history traits and evolutionary age remains poorly understood. Here, we map the geographical variation in the proportions of different sexual systems and hypothesize that the decreasing prevalence of hermaphrodites with increased humidity is due to their advantages in colonizing harsh environment, whereas dioecy is most successful in humid regions with tall-canopy vegetation and old floras.

Location: China

Time period: Current

Major taxa studied: Flowering woody plants

Methods: Using data on sexual systems and distributions of 10,449 woody species in China, we estimated the proportions of different sexual systems in local floras (50 × 50 km grid cells). Spatial linear models, phylogenetic general linear models and structural equation models were used to compare the relative influences of climate, plant height and evolutionary age on geographical variation in the proportions of different sexual systems.

Results: We found contrasting geographical patterns in the proportions of different sexual systems. The proportions of dioecy and monoecy increased with plant height and were highest in humid regions with older floras, while that of hermaphroditism decreased with plant height and was highest in arid regions with younger floras. Plant height was the strongest correlate of sexual system frequency. Climate influenced sexual system frequency both directly and indirectly via its effects on plant height.

Main conclusions: Our study provides the first continuous map of sexual system composition in woody floras over a large spatial scale. Our findings suggest that mature plant height, reflecting plant longevity, dominates geographical variation in sexual systems and that the proportions of different sexual systems in local floras may reflect correlated evolution with traits that are tied closely with sexual systems in response to climate warming.

Keywords: angiosperms, China, climate change, evolutionary history, geographical pattern, macro evo-devo, plant height, plant reproduction, sexual systems

INTRODUCTION

Plants exhibit remarkable variation in their sexual systems, which act as a major driver of the genetic and evolutionary dynamics of angiosperms (Barrett & Harder, 1996; Charlesworth, 2006), as well as having considerable ecological significance (e.g., pathogen resistance, Williams, 2011; herbivore resistance, Campbell & Kessler, 2013). Selective pressures on sexual systems vary with environmental conditions (Barrett, 1998; Ricklefs & Wikelski, 2002; Jacquemyn et al., 2005; Dorken, Freckleton, & Pannell, 2017), potentially leading to geographical variation in the composition of sexual systems in local floras. Although a few studies explored changes in sexual systems using sparse data at restricted spatial scale (Lloyd, 1980; Jacquemyn et al., 2005; Moeller et al., 2017), to date potential drivers of these biogeographical patterns of sexual systems have rarely been investigated (Matthew et al., 2016). Contemporary climate, plant life-history traits, and the evolutionary age of floras may all influence the composition of sexual systems. However, the relative contributions of these drivers to the biogeographical patterns of plant sexual systems remain poorly understood.

Climate can influence the expression of plant sexual systems by regulating the allocation of resources to female and male function during the flowering period (Zhang, 2006) and hence can lead to geographical variation in the composition of sexual systems of local floras (Freeman et al. 1976; Barrett, 1998; Ricklefs & Wikelski, 2002; Jacquemyn et al., 2005; Hultine et al., 2016; Dorken, Freckleton, & Pannell, 2017). For example, recent studies found that the proportion of outcrossing species decreased with latitude (Moeller et al. 2017), which has been attributed to changes in precipitation, temperature, and solar radiation along the latitudinal gradient (Lyold, 1980). However, previous studies provided controversial evidence

on the effects of climate, especially the effects of water availability, on the biogeographical patterns of plant sexual systems. First, some studies explored the evolution of sexual systems and indicated that drought stress might have contributed to the evolution of dioecy from hermaphroditism (Webb, 1999; Ashman 2006; Yang et al. 2014), which suggested that the prevalence of dioecy could be associated with arid environment. Second, other studies suggested that the colonization to dry habitats does not require a shift to sex dimorphism (Sakai et al. 1997), because spatial separation likely makes dioecious taxa suffer greater challenges of decreased mate assurance (Pannell & Barrett 1998). Compared with dioecious taxa, hermaphroditic species likely have been selected in stressful regions with frequent extinction and re-colonization (Obbard et al. 2006; Levin, 2012), because hermaphrodites can provide reproductive assurance via selfing (Lloyd, 1992; Harder & Barrett 1995; Barrett, 1998; Elle & Carney 2003). Studies based on field investigations found that hermaphroditic species from different clades widely occured in dry habitats while dioecious species were more common in humid and tropical regions (Freeman et al., 1980; Sakai & Wagner, 1995; Matallana et al. 2005). Although these findings tend to support the second hypothesis, how sexual system composition varies geographically with climate, especially with water availability, still remains controversial.

Plants with different life-history traits vary considerably in their sexual systems (Barrett & Eckert, 1990; Snell & Aarssen, 2005; Moeller et al., 2017), which suggests that plant life-history traits also likely influence the ecology and evolution of sexual systems (Vamosi et al. 2003). Phylogenetic analyses have revealed the association between dioecy and woody growth habit (i.e., the long-lived, perennial growth form) (Chazdon et al. 2003; Vamosi et al.

2003). Similarly, longevity has been found to be an important trait associated with plant sexual systems (Renner, 2014). Compared with short-lived species, long-lived ones tend to accumulate more genetic load (Klekowski & Godfrey, 1989), to pay a higher fitness cost due to inbreeding depression and mutation, and to depend more on cross-pollination (Klekowski & Godfrey, 1989; Chen, 2003). Consequently, dioecy is more common in long-lived species than in short-lived ones (Renner & Ricklefs, 1995; Renner 2014). In contrast, short-lived species have limited time to find mates, reproduce, and complete their life cycle, hence, they tend to contain a larger proportion of selfing species (i.e. hermaphrodite and monoecy) relative to long-lived species (Morgan et al., 1997; Aarssen, 2000).

Evolutionary history has been found to shape the distribution of sexual systems across the phylogeny of seed plants (Lord et al., 1995; Renner & Ricklefs, 1995). For example, significant phylogenetic signals were detected in the sexual systems of 641 species distributed in the Yasuní National Park, Ecuador (Queenborough et al., 2009). Previous evolutionary studies suggest that dioecious species have been derived from hermaphroditism and that dioecious lineages are most often at the tips of angiosperm phylogenies (Barrett 2013). According to this hypothesis, the prevalence of dioecious and hermaphroditic species in local floras should negatively correlate with flora age. More specifically, it may be expected that dioecious species are more prevalent in young floras while hermaphroditic species are more prevalent in old floras. However, in contrast to the predictions of this hypothesis, field investigations based on scattered data found that dioecious species are more common on old than on young islands (Sakai et al. 1995) and in tropical areas (Matallana et al. 2005) dominated by old floras than in temperate areas with young floras. These findings

104 demonstrate that the relationship between the prevalence of a particular sexual system and
105 evolutionary age of floras so far remains inconsistent from an evolutionary and an ecological
106 perspective. Here we maintain that it is necessary to explore this relationship more
107 comprehensively across larger geographical scales to derive generalities.
108 With this goal in mind, we compiled data for sexual systems of woody angiosperms
109 spanning a broad environmental gradient in China. By combining these data with high-
110 resolution species distribution maps, we explored the geographical variation in the
111 composition of sexual systems of woody plants in China and their potential abiotic (climatic)
112 and biotic (plant traits and evolutionary age) drivers. Specifically, we aimed to test the
113 following three hypotheses: 1) the proportion of dioecy in floras increases, whereas the
114 proportion of hermaphroditism decreases with humidity. 2) dioecy is positively and
115 hermaphroditism negatively related to longevity across regions. 3) dioecy is most successful
116 in old woody floras, whereas hermaphroditism dominates young ones.
117
118 **MATERIALS AND METHODS**
119 **Sexual systems and distributions of woody plants in China**
120 We compiled a dataset on the sexual system of all woody plant species in China using
121 published sources: Flora of China (Wu, Raven & Hong, 1994-2013), Flora Republicae
122 Popularis Sinicae (126 issues of 80 volumes), Seeds of Woody Plants in China, eflora
123 (http://efloras.org/), Tree of Sex (Ashman et al., 2014), Plant Trait Database (TRY, 2012),
124 Botanical Information and Ecology Network (BIEN, Enquist et al., 2016) and journal
125 publication (Goldberg et al., 2017). For species for which the sexual system was reported in

multiple sources, those with conflicting reports were checked and corrected or removed. In total, our dataset comprises 10,449 species from 1,082 genera and 157 families, and accounts for 93.76% of all woody plants found in China (Table S1). We classified all these species into three categories based on their sexual system following Cardoso et al. (2018): dioecy (i.e. plant species with separate male and female individuals), monoecy (i.e. plant species with both staminate and pistillate flowers occurring in the same individual but not in the same flower), and hermaphrodites (i.e. plant species with both functional stamens and pistils in the same flower). The category of dioecy includes androdioecious, gynodioecious and polygamodioecious species, while monoecy includes monoecious, andromonoecious and gynomonoecious species.

The sexual systems of a few species likely vary (e.g., Schoen, 1982; Dorken, Freckleton, & Pannell, 2017) in response to local abiotic or biotic conditions (e.g., climate variables or pollinator densities; Barrett & Harder, 2017). Such species were excluded from the final dataset used in this study.

The distribution data of woody plants across China were taken from the Atlas of Woody Plants in China (Fang et al., 2011), which contains the distribution of all the 11,405 woody species (see Wang et al., 2009, for details). Species distributions were further checked and supplemented using recently published specimen records (see http://www.nsii.org.cn/).

Geographical variation in the proportions of different sexual systems

We first transformed the distribution maps into equal-area grids with grid cell size of 50 × 50 km to eliminate the potential bias of unequal area on subsequent analyses (see Wang et al.,

2009, for details). Combining the sexual-system data and the distribution data of all species, we calculated the proportions of species with each sexual system type within every grid cell. To ensure the reliability of the calculated proportion for each sexual system, we removed grid cells with less than half of the grid cell area (i.e. grid cells with < 1250 km^2, see Wang et al., 2009, for details), and grid cells with fewer than 10 woody species. A total of 3,539 out of initially x,xxx grid cells were finally included in the analyses.

Climatic data

To evaluate the effects of climate on the biogeographical pattern in the composition of sexual systems in different local floras we used climatic data with a spatial resolution of 1 × 1 km for the period 1950–2000 obtained from WorldClim (Hijmans et al., 2005). We obtained the value of every climate variable for each 50 × 50 km grid cell by calculating the average of all 1 × 1 km cells within it. Climatic variables were categorized into temperature, precipitation and solar radiation. Temperature variables included mean annual temperature (MAT), mean temperature of coldest quarter (MTCQ) and annual potential evapotranspiration (PET). PET reflects the amount of evaporation that would occur if sufficient water were available and was calculated following the method of Thornthwaite (1955). Precipitation variables included mean annual precipitation (MAP), precipitation seasonality (PSN, the coefficient of variation of mean monthly precipitation) and Precipitation of Driest Quarter (PDQ). Solar radiation reflects the radiant energy emitted by the sun. MAP and PDQ were natural-logarithm transformed because of their left-skewed distributions. Solar radiation likely influences flower coloration through pigmentation, which further affects pollination success (Körner, 1999).

The average and the full range of values for each climatic variable within each grid cell were estimated with the zonal statistics tool in ArcGIS 10.0.

In China, the 800-mm isoline of MAP coincides with the 0 °C isotherm of mean minimum January temperature and is the boundary between non-humid (or semi-humid) areas (including deserts, grasslands and temperate forests) and humid areas (including subtropical and tropical evergreen broad-leaved forests). We used this isoline to evaluate the comprehensive effects of climate on the distributions of sexual systems.

Mature plant height

Because height is strongly associated with the longevity of woody plant species (Marbà et al. 2007; Moles and Leishman, 2008; Moles et al. 2009), we used the mature plant height as a proxy for longevity to test hypotheses related to longevity. Mature plant height data were extracted from the Flora of China (http://frps.eflora.cn/, accessed in November 2013; http://www.efloras.org/flora_page.aspx?flora_id=2, accessed in February 2014). For species with more than one record of the height of mature individuals, we used the average of these records. Species without erect stems (e.g., woody lianas, climbers, scandent shrubs or epiphytes) were excluded from our database following Moles et al. (2009). We then averaged the mature height across all species within each grid cell to examine the effect of plant height on the biogeographic patterns of sexual systems.

Genus age

Clade age (e.g. family age and genus age) has been widely used in various large-scale studies such as testing the niche-conservatism hypothesis (Leopold et al. 2015; Qian 2014, 2017;

193 Qian et al. 2017; Lu et al. 2018). Genus has been considered to be more natural than other
194 taxonomic ranks (Anderson, 1940), so we only used genera that have been proven to be
195 monophyletic by phylogenetic trees based on molecular data.

196 To evaluate the effect of evolutionary age on the biogeographical pattern of sexual
197 systems (the grid-level proportions of the three sexual systems), we extracted the genus age
198 from the genus-level tree of Chinese vascular plants constructed by Chen et al. (2016) and
199 calculated the average genus age for each grid cell. These analyses were performed in R 3.3.1
200 (R Core team 2016).

201

202 **Statistical analyses**

203 First, spatial linear models (SLM) were built to evaluate the relative importance of climatic
204 variables (temperature, precipitation and radiation), mature plant height and average genus
205 age per grid cell in determining the biogeographical pattern in sexual systems. Spatial
206 simultaneous autoregressive error models (SARs) allowing the inclusion of residual spatial
207 autocorrelation in data (Kissling & Carl, 2008) were used for the SLMs. Moran's I was used
208 to diagnose the spatial autocorrelation of residuals of SLMs. Using this approach, we could
209 ensure that the spatial autocorrelation had been successfully removed ($P > 0.05$ in all cases).

210 To evaluate the effect of phylogenetic conservatism on the distribution of sexual systems
211 of woody plants, we first calculated the proportions of species with different sexual systems
212 for each genus separately. Then, we estimated Blomberg'*K* (Blomberg et al., 2003) for each
213 sexual system separately at the genus level using the "phylosignal" function (Keck et al.,
214 2016) in the R package "*picante*". The sexual systems of different species are not

phylogenetically independent from each other (Table 2). To account for the influence of phylogenetic dependence of sexual systems on the relationships between the grid-level proportions of the three sexual systems and predictors, we fitted a phylogenetically corrected linear mixed-effects model by maximum likelihood ("lmekin" within the R package "*coxme*"; Orme, 2012).

To further compare the effects of abiotic (climate) and biotic drivers (plant height and genus age) on the biogeographical pattern in sexual systems, we generated structural equation models (SEM) by assuming that plant height and genus age influence distributions of sexual systems directly, while the climate variables could influence distributions of sexual systems both directly and indirectly via their effects on plant height (Moles et al., 2009).

The above analyses were undertaken with principal component scores (PCs) derived from principal component analysis (PCA, using the "princomp" function in R, Conway & Huffcutt, 2003) (SLM, lmekin and SEM). One PCA was used to combine the temperature variables (MAT, MTCQ and PET) into a single PC (Temp.PC1) and another one was used to combine the precipitation variables (MAP, PSN and PDQ) into Prec.PC1 (Table S2). The first principal components accounted for 93.6% and 78.3% of the variations in temperature and precipitation variables, respectively. Pearson correlations among the two PCs and solar radiation, plant height and genus age were lower than 0.7, indicating a relatively low level of multicollinearity (Dormann et al., 2013). Based on these data explorations Temp.PC1, Prec.PC1, solar radiation, plant height and genus age were included in the final SLM, lmekin and SEM analyses (Table1 & Fig. 2).

RESULTS

Biogeographical patterns in sexual systems

Overall, hermaphroditism is the most common sexual system of woody plants across China: the proportion of hermaphrodite species is ≥ 50% in 96.1% of the grid cells (Fig. 1). The proportion of dioecious but not of monoecious species is strongly negatively correlated with the proportion of hermaphrodite species (Fig. S1). The relative frequency of the three sexual systems varies geographically (Fig. 1). The proportion of dioecious species is high in northeast China and the Qinghai-Tibetan Plateau whereas the proportion of monoecious species is high in eastern and southern China. In contrast, the proportion of hermaphrodites is high in northwest China (Fig. 1c).

Influence of climate on sexual systems: role of humidity

Temperature (Temp.PC1) had weak effects on the composition of sexual systems, both with or without controlling for other explanatory variables in SAR (Table 1 & S3). In SEM, the influence of temperature on proportions of dioecious and hermaphroditic species was strong in non-humid areas, indicating that correlations between plant height and temperature may have masked temperature effects (Fig. 3). Precipitation affected the prevalence of particular sexual systems weakly in both non-humid and humid areas (Table 1). Solar radiation also had weak effect on the composition of sexual systems (Table 1). After controlling for the effect of climate on plant height in the SEMs, in the humid area radiation significantly negatively affected dioecy and monoecy and positively affected hermaphroditism (Fig. 3).

Influence of mature plant height as a proxy for longevity on sexual systems

Sexual-system composition varied with plant height (Fig. 2). The proportions of hermaphrodite species decreased with plant height, that is, shorter plants (e.g., < 5 m) had a disproportionately high proportion of hermaphrodites. In contrast, the proportions of dioecious and monoecious species increased with plant height (Table 1).

Average plant height per grid cell had consistently the highest explanatory power for geographical variation in composition of sexual systems, both with or without controlling for other predictors (Table 1 & S4; Fig. 3).

Influence of evolutionary age on sexual systems

Blomberg's K indicated significant phylogenetic signal in the within-genus proportion of dioecious species ($P < 0.001$), suggesting that dioecy in woody plants is phylogenetically conserved, and closely related genera tend to have similar proportions of dioecy. In contrast, the monoecious and hermaphroditic proportions had no significant phylogenetic signal ($P > 0.05$, Table 2).

Whether controlling or not for phylogeny or other predictors, average genus age per grid cell was significantly but weakly correlated with biogeographical patterns of sexual systems in both non-humid and humid areas (Table 1 & S3; Fig. 2).

DISCUSSION

In this study, we investigated the geographical variation of sexual systems of woody plants in China and the mechanisms shaping this variation. We found that climate mainly influenced

281 the biogeographical pattern of sexual systems indirectly by affecting plant height, which we
282 used as a proxy for longevity. Plant height had consistently the highest explanatory power for
283 the proportions of sexual systems across regions. Our findings are thus consistent with the
284 idea that biogeographical patterns in sexual systems reflect longevity (Renner, 2014). Our
285 results also revealed significant contributions of climate and evolutionary age to geographical
286 variation in sexual systems.

287

288 **Influence of mature plant height on sexual systems**

289 The geographical variation in the proportions of different sexual systems across China are
290 predominantly driven by variations in plant height (see Fig. 1 & S4). This is extends previous
291 findings that the frequency of life forms correlates with the frequency of mating systems
292 across latitude (Moeller et al., 2017) or that the proportion of dioecious species is higher
293 among trees than among other lifeforms (e.g. Bawa et al., 1985; Renner & Ricklefs, 1995)
294 and higher in canopy (24.5%) than in understory species (9.8%) (Kress & Beach 1994).
295 Previous studies also found that large plants tend to have larger flower size and number of
296 floral structures (e.g., petals and stamens) than small plants (Méndez & Traveset, 2003),
297 which may intensify the disadvantages of self-incompatibility and benefit cross-pollination in
298 dioecious species (Harder & Barrett, 1995), especially during mass-flowering events (Eckert
299 et al., 2000). In contrast, selection pressure may be expected to increase the proportion of
300 selfing hermaphrodites among small plants.

301 Given the well-documented association between plant height and longevity (Marbà et
302 al. 2007; Moles and Leishman, 2008; Moles et al. 2009), our results also suggest an

303 association between sexual systems and longevity, in particular increased frequency of dioecy
304 and monoecy. Our results thus generalize previous findings about a positive association
305 between dioecy and plant longevity at family level (Renner, 2014) to the species level and
306 monoecy. In contrast, short-lived species are expected to have higher frequency of
307 hermaphrodites, which may explain a higher frequency of hermaphrodites in temperate
308 regions as compared with sub-tropical and tropical regions (Moeller et al., 2017).
309
310 **Influence of climate on the proportions of sexual systems**
311 Our results are consistent with previous findings that mating strategies of woody plants are
312 sensitive to variations in contemporary climate (reflected by both temperature and
313 precipitation) across space (Waller, 1980; Chaves et al., 2003; Dorji et al., 2013; Etterson &
314 Mazer, 2016). However, the effects of climate on the proportions of different sexual systems
315 tended to be indirect since we found that climate had weak direct effects on the
316 biogeographical patterns of sexual systems in both SLMs and SEMs (see Table 1 & Fig. 3).
317 We found that the proportions of hermaphroditic plants were highest in drylands in western
318 China (see Fig. 1), suggesting that hermaphrodites have better drought tolerance than
319 dioecious and monoecious species (Verdú 2004; Obbard et al. 2006). Hermaphrodites are
320 often selfers (Peng et al., 2014, Moeller et al., 2017) and selfers have been found to be able to
321 accelerate carbon assimilation rates, flower early and complete their life cycle rapidly (Mazer
322 et al., 2011. Guerrant, 1989), potentially reducing their exposure to drought in drylands (Ivey
323 et al., 2016). Solar radiation may affect the relative representation of sexual systems via its
324 influence on flower coloration (Peng et al., (2014). For example, Peng et al. (2014) found that

hermaphroditism was associated with strong flower color in alpine plants. Quantifying the influence of solar radiation on the frequency of different sexual systems via flower coloration deserves further study.

Evolutionary history of sexual systems

We found a significant phylogenetic signal in the genus-level proportions of dioecy, suggesting that the evolution of dioecy has been phylogenetically conserved through evolutionary history (Chazon et al. 2003). In contrast, the genus-level proportions of monoecy and hermaphroditism had very low and non-significant values of Blomberg's K, indicating that monoecious and hermaphroditic species likely have evolved independently many times and possibly for different reasons (Lloyd, 1982).

However, genus age correlated only weakly with the biogeographical pattern of sexual system composition across China (see Table 1 & Fig. S2). For example, the proportion of hermaphroditic species was highest in northwest China where woody floras are relatively young (Lu et al., 2018), which support the idea that hermaphrodites have been selected in regions with frequent extinction and re-colonization. In contrast, higher proportions of dioecy may only have been maintained in regions with low rates of local extinction and re-colonization, due to the limitation of mating opportunities (Obbard et al., 2005). This may explain the high proportion of dioecious species in northeast China where woody floras are relatively old (Lu et al., 2018). The relationship between sexual system composition and clade age in a region may be confounded by the magnitude and velocity of climate change, life-history strategies, local adaptation and generation times (Qian 2014, 2017; Hultine et al.,

2016).

Comparison of sexual systems of woody species

Although previous studies have noted phylogenetic patterns in the distribution of dioecy, monoecy and hermaphroditism, little has been known about the association between ecological conditions and the distribution of different sexual systems. We found clear evidence that dioecious and hermaphroditic species are favored by opposite ecological conditions: the proportion of dioecy decreased with radiation but increased with plant height and genus age, while that of hermaphroditism showed the opposite trends (see Table 1). This finding suggests that dioecy and hermaphroditism are two evolutionary extremes of adaptation to specific selection pressures (e.g., climate) during evolutionary history (Snell & Aarssen, 2005; Cannon & Lerdau, 2015; Moller et al., 2017).

Biogeographical patterns in the proportion of monoecious species were more comples than those of the other two sexual systems. In Costa Rica, Vamosi & Queenborough (2010) found a comparable reliance of dioecious and monoecious species on insect and wind pollination in a series of forest plots along a local transect. This may be due to more common wind dispersal in dry forests, which has lower metabolic costs of producing nectar and fleshy fruit, while more expensive insect pollination could ensure reproductive success in wet tropical forests (Rech et al. 2016). Here we found that the proportions of dioecious and monoecious species consistently increased with the average plant height per grid cell. But we also found that the proportion of monoecy responded to climate (precipitation in arid area and radiation in humid area) in a similar way as the proportion of hermaphrodites did. These results may indicate that monoecy

adapts to specific ecological conditions flexibly or that monoecy is an intermediate stage between the other two sexual systems (Goldberg et al., 2017) and thus not so clearly associated with particular environmental conditions. It is noteworthy that many previous studies about the distribution of sexual systems have pooled monoecious and hermaphroditic species together (e.g. Dorken, Freckleton, & Pannell, 2002; Vamosi et al., 2008; Queenborough et al., 2009). As a result, the ecological and evolutionary aspects of monoecy have been understudied in relation to dioecy and hermaphroditism.

Caveat to correlative studies

Although correlative studies have the disadvantage that they can only test potential causal relationships, they have the advantage that they can be based on large amounts of data collected under natural conditions. Thus, our analyses offers valuable insights into correlations that can be used to derive to causal hypotheses about the potential effects of abiotic (climate) and biotic (plant height, genus age) drivers of geographical variation in angiosperm sexual system. Experimental tests would require large-scale transplantation studies. In addition, species extinctions and ongoing and future climate change, respectively, may provide perhaps unwelcome natural experiments to test these biotic and abiotic hypotheses.

Conclusions

Our findings suggest that mature plant height is the strongest predictor of the biogeographical pattern of woody angiosperm sexual systems across local floras in China and that climate also

391 plays an important role, whereas genus age has a relatively weak influence. The proportions
392 of dioecy and hermaphrodites in local floras had opposite trends along abiotic and biotic
393 drivers, suggesting that these two sexual systems may represent opposite directions of
394 evolution in adapting to environmental pressures. The flexible response of monoecy to
395 ecological conditions compared with dioecy and hermaphrodite deserves further investigation
396 due to the intermediate state of monoecy between the other two. Our findings shed light on
397 the ecological drivers of geographical variation in sexual systems of woody plants across
398 China and suggest that environmental adaptation significantly influences the biogeographical
399 pattern of sexual systems. Moreover, our finding that present-day geographical variation in
400 sexual system distribution is strongly related to contemporary climate variables suggests that
401 the composition of sexual systems in local floras may be sensitive to global climate change,
402 and different responses of different sexual systems to ongoing and future climate change
403 could lead to significant changes in the species composition in local plant communities.
404

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566

Conflict of interest statement

The authors declare that they have no conflict of interest.

Data accessibility

Should the manuscript be accepted, the data supporting the results in the paper will be archived in Dryad and the data DOI will be included at the end of the article.

TABLES

Table 1 Spatial linear models (SLMs) with simultaneous autoregressive errors (SAR) for proportions of sexual systems as the dependent variable and climate variables (temperature, precipitation and radiation), mature plant height and genus age as multiple independent variables. We show the partial regression coefficients with their standard errors for the explanatory variables. The table shows results from entire China, the area with less than 800 mm precipitation (non-humid area), and the area with over 800 mm precipitation (humid area). Values in bold are significant at $P < 0.05$ and three relevant digits were presented for all the values. MHt - mature plant height; Herma - Hermaphrodite. Moran's I test showed that there was no residual spatial autocorrelation left after the SAM correction.

Variable	Entire area			Non-humid area			Humid area		
	Dioecy	Monoecy	Herma.	Dioecy	Monoecy	Herma.	Dioecy	Monoecy	Herma.
Temp.PC1	-0.00207	**0.00509**	0.00204	-0.00110	**0.00402**	-0.00101	0.00091	0.00145	<0.0001
Prec.PC1	<0.0001	-0.00151	0.00145	0.00467	-0.00100	-0.00212	-0.00196	-0.00104	0.00308
Radiation	-0.00146	**-0.00579**	0.000643	-0.00482	**-0.00679**	0.00584	-0.00291	0.00171	**0.00890**
MHt	**0.0390**	**0.0116**	**-0.0523**	**0.0381**	**0.00967**	**-0.0520**	**0.00458**	**0.00817**	**-0.0189**
Genus age	**0.00276**	**0.00406**	**-0.00687**	0.00206	**0.00485**	**-0.00677**	**0.00476**	0.00057	**-0.00596**
Pseudo-R^2	0.83	0.82	0.89	0.84	0.77	0.89	0.68	0.67	0.79
Moran's I	0.013	0.010	0.010	0.013	0.010	0.010	0.020	<0.001	0.020

Table 2 The influence of genus age on the patterns of sexual system proportions. Blomberg's *K* for both within-genus and within-family proportions of species with different sexual systems. The genus-level phylogenetic tree was extracted from the genus-level tree of Chinese vascular plants constructed by Chen et al. (2016).

Sexual system	Phylogenetic Signal	*P* value
Dioecy	0.493	**0.0001**
Monoecy	0.156	**0.307**
Hermaphrodite	0.165	**0.526**

FIGURES

Figure 1. Spatial patterns in the proportion of angiosperm species with different sexual systems: (a) dioecy; (b) monoecy; (c) hermaphrodites. The solid black line in the figures is the isoline of mean annual precipitation of 800 mm, which also closely tracks to the isoline of mean annual temperature of 0 °C. Grid cells with fewer than 10 woody species are shown in grey.

Figure 2 Comparison between the proportions of species with different sexual systems across different plant heights. Corresponding plant heights are shown under the x axis. Here panel (a) represents the whole study area, (b) represents the area with yearly precipitation < 800 mm (non-humid area), and (c) represents the area with precipitation > 800 mm (humid area).

Figure 3 Path diagrams showing interactions among climate (the first principal components of temperature [T.PC1] and precipitation [P.PC1] and solar radiation [RAD]), mature plant height (Height) and genus age (Age), and proportions of sexual systems. The values next to the arrows are standardized path coefficients. Red values indicate positive relationships and blue values indicate negative relationships. The line thickness of path arrows represents the strength of the relationship. The paths with $p > 0.05$ are not shown. Mono. = Monoecy, Herma. = Hermaphrodite.

Figure 1

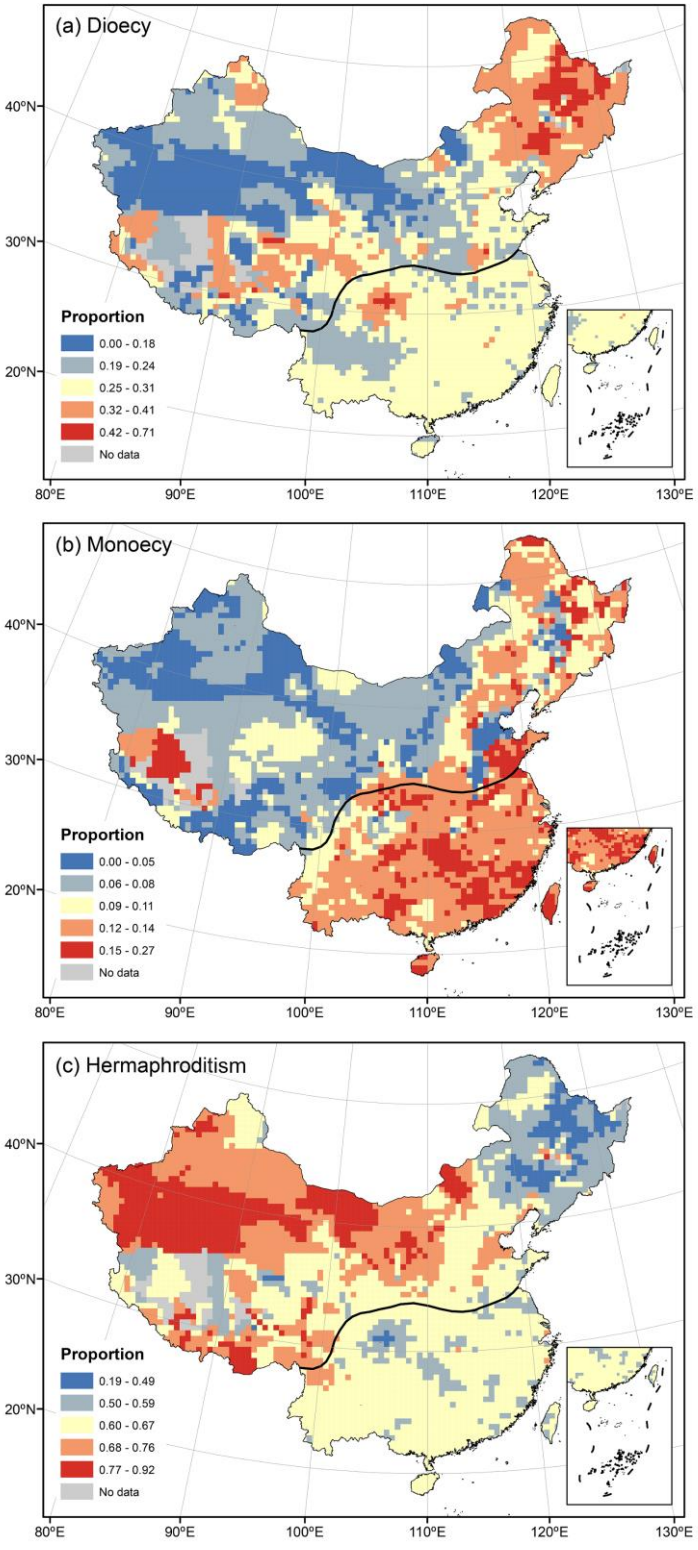

(a) Dioecy
Proportion
0.00 - 0.18
0.19 - 0.24
0.25 - 0.31
0.32 - 0.41
0.42 - 0.71
No data
(b) Monoecy
Proportion
0.00 - 0.05
0.06 - 0.08
0.09 - 0.11
0.12 - 0.14
0.15 - 0.27
No data
(c) Hermaphroditism
Proportion
0.19 - 0.49
0.50 - 0.59
0.60 - 0.67
0.68 - 0.76
0.77 - 0.92
No data
40°N
30°N
20°N
80°E
90°E
100°E
110°E
120°E
130°E

Figure 2

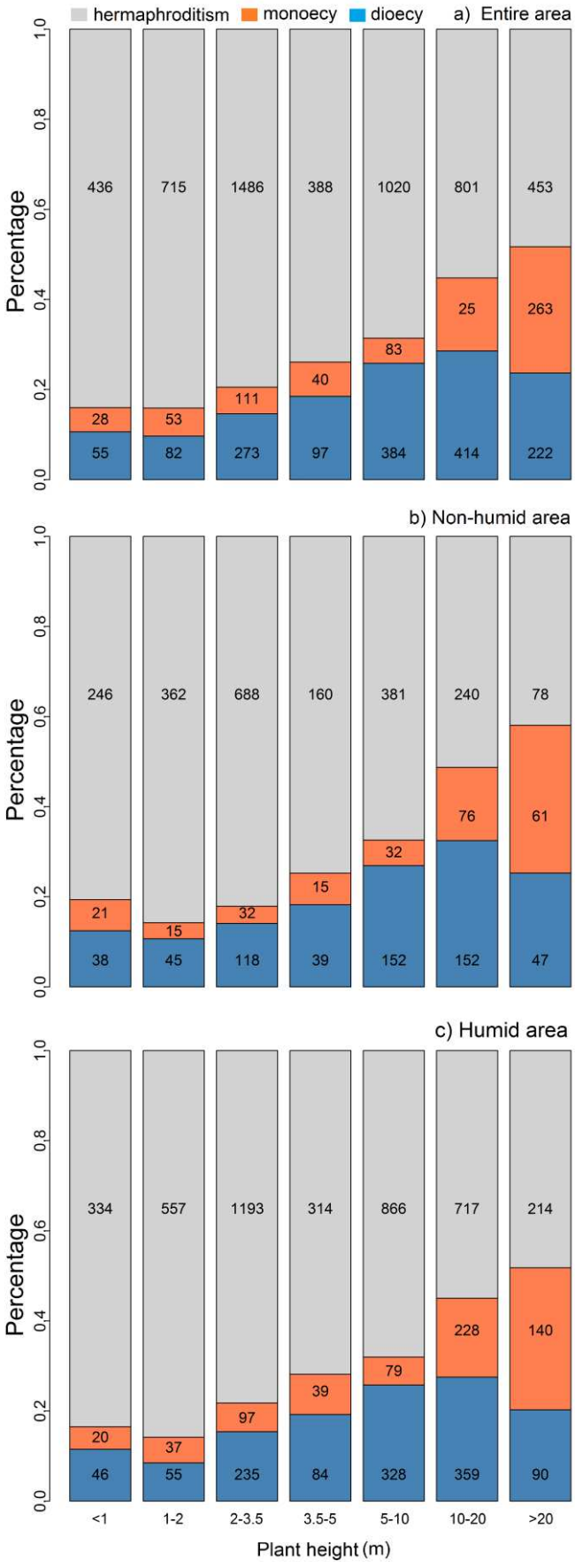
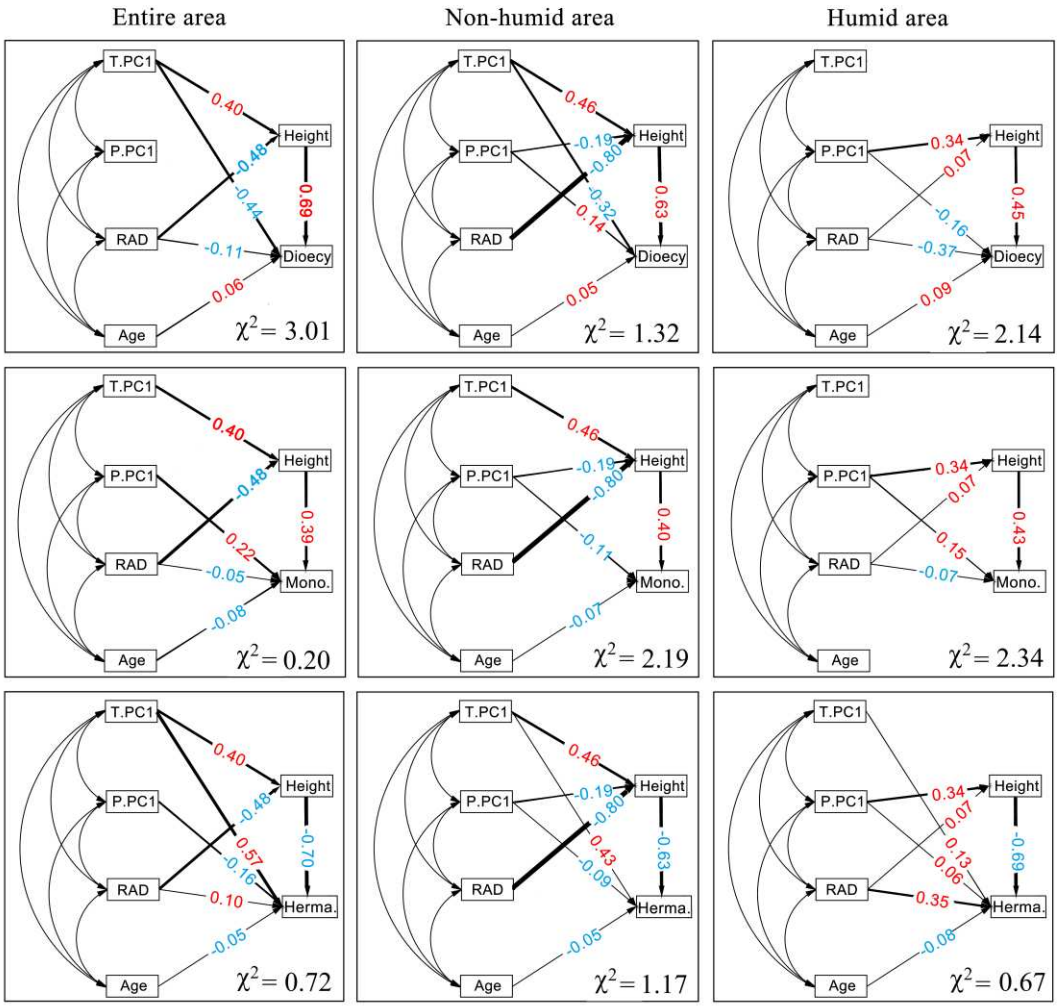

hermaphroditism
monoecy
dioecy
a) Entire area
b) Non-humid area
c) Humid area
Percentage
0,0
0,2
0,4
0,6
0,8
1,0
436
715
1486
388
1020
801
453
28
53
111
40
83
25
263
55
82
273
97
384
414
222
246
362
688
160
381
240
78
21
15
32
15
32
76
61
38
45
118
39
152
152
47
334
557
1193
314
866
717
214
20
37
97
39
79
228
140
46
55
235
84
328
359
90
<1
1-2
2-3.5
3.5-5
5-10
10-20
>20
Plant height (m)

Figure 3


Entire area
Non-humid area
Humid area
T.PC1
P.PC1
RAD
Age
Height
Dioecy
Mono.
Herma.
0.40
-0.48
-0.44
0.69
-0.11
0.06
$\chi^2 = 3.01$
0.46
-0.19
-0.80
-0.32
0.14
0.63
0.05
$\chi^2 = 1.32$
0.34
0.07
-0.16
-0.37
0.45
0.09
$\chi^2 = 2.14$
0.40
-0.48
0.22
0.39
-0.05
-0.08
$\chi^2 = 0.20$
0.46
-0.19
-0.80
-0.11
0.40
-0.07
$\chi^2 = 2.19$
0.34
0.07
0.15
0.43
-0.07
$\chi^2 = 2.34$
0.40
-0.48
0.57
-0.16
-0.70
0.10
-0.05
$\chi^2 = 0.72$
0.46
-0.19
-0.80
0.43
-0.09
-0.63
-0.05
$\chi^2 = 1.17$
0.34
0.07
0.13
0.06
-0.69
0.35
-0.08
$\chi^2 = 0.67$